Spatial variation in life history characteristics of waved whelk (*Buccinum undatum* L.) on the U.S. Mid-Atlantic continental shelf

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Abstract

Recent expansion of the unmanaged waved whelk (*Buccinum undatum*) fishery within the United States Mid-Atlantic continental shelf region has prompted investigation into local life history parameters. Limited adult dispersal and lack of a planktonic larval stage has the potential to create spatially distinct populations with respect to size of sexual maturity and size frequency. During the summer of 2015, a comprehensive survey was undertaken to evaluate population structure, sex ratio, relative abundance and size of sexual maturity for waved whelk in the Mid-Atlantic. Samples (n=254) were collected from Georges Bank through the DelMarVa region using a modified scallop dredge at depths ranging from 27.4 to 112 m, with most whelk caught between 40 to 75 m, and peak abundances at 51 to 60 m. All whelk collected (n=3,877) were sexed, weighed, measured, and assessed for maturity. Sex ratios were skewed in favor of females in the south, and balanced through the rest of the region. Size of maturity ranged from approximately 56 to 73 mm, and varied among regions and sex. Estimates of size of sexual maturity for *B. undatum* from other regions of the world were compiled, demonstrating that the size of maturity for this species is highly variable, and current minimum landing size regulations tend to fall below the estimated size of sexual maturity, potentially increasing the risk of recruitment overfishing. Overall, spatial variation in whelk phenotype suggests local adaptation in this species, indicating that regional management would be most appropriate.

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1. Introduction

The waved or common whelk (*Buccinum undatum*) is a subtidal, carnivorous gastropod that is widely distributed throughout the North Atlantic Ocean and adjoining seas. Several key fisheries for this species occur in coastal waters around Canada, France, the Republic of Ireland, and the United Kingdom (Fahy et al., 2000; Heude-Berthelin et al., 2011; Jalbert et al., 1989; Nasution and Roberts, 2004; Shelmerdine et al., 2007). Global expansion of the fishery began in the 1990's in response to increased market demand (Fahy et al., 2000). Currently, the species remains unregulated in the Mid-Atlantic waters of the United States, the southern extent of the species' range, but fishery development is starting to occur. Recent landings of *B. undatum* have fluctuated in the U.S., with a peak of 1571.8 mt in 2013, and declining to 21.6 mt in 2015 (NOAA Analysis and Program Support Division, pers. comm.). As commercial demand and interest in this fishery continues, it is critical to obtain baseline life history information to inform stock assessment and support fishery management.

Waved whelk exhibit limited dispersal potential, with relatively sedentary adults and intracapsular larval development resulting in crawl-away juveniles (Hancock, 1963; Himmelman and Hamel, 1993; Shelmerdine et al., 2007). These life history traits have the potential to limit mixing between populations, resulting in locally distinct morphological and genetic characteristics, both of which have been observed across small spatial scales (Gendron, 1992; Shelmerdine et al., 2007; Valentinsson et al., 1999; Weetman et al., 2006). This limited connectivity could mean that this species is particularly susceptible to localized depletion, and may experience protracted recovery times if overfishing were to occur (Himmelman and Hamel, 1993; Weetman et al., 2006).

Minimum landing size (MLS) is a common fisheries management approach, implemented to protect spawning stocks, with the intent commonly to limit the impact of fishing mortality on immature individuals. A common management strategy in *B. undatum* fisheries is the use of a broad-based MLS, in which one national minimum landing size regulation is applied to an entire region or country (Fahy et al., 1995; Gendron, 1992). This approach, however, may not fully account for fine spatial scale changes in biological characteristics across fishing regions and therefore may not fully protect the exploited stock (Fahy et al., 2000; Haig et al., 2015; Heude-Berthelin et al., 2011). Recommendations have been made to manage on a finer spatial scale and utilize MLSs appropriate for different fishing areas based on local biology (Kenchington and Glass, 1998; Shelmerdine et al., 2007). Some regional MLS management measures have been enacted in an attempt to better protect local populations (McIntyre et al., 2015). Throughout the E.U., the baseline MLS is 45 mm shell length. However, many local fisheries agencies have increased the MLS after local studies of size of maturity were performed, opting for larger regional MLS regulations to protect spawning stock biomass (Kideys, 1996; Morel and Bossy, 2004; Shelmerdine et al., 2007). For example, the Shetland Islands have increased local MLS (6 mile radius) from 45 to 75 mm shell length (Shelmerdine et al., 2007).

This study describes the population structure of *B. undatum* in the United States Mid-Atlantic and compares the results to other assessed populations via an examination of the species range, size structure, sex ratio, and size of sexual maturity. Using other managed *B. undatum* populations as examples, we discuss whether a national (broad-based) MLS provides sufficient protection to the spawning stock and decreases the probability of recruitment overfishing in the *B. undatum* fishery.

2. Methods

The Mid-Atlantic continental shelf includes a wide range of habitats with diverse physical and biological properties (Stevenson et al., 2004). The current study focused on two principle systems within the Northeast U.S. shelf: Georges Bank and the Mid-Atlantic Bight. Georges Bank (GB) is a relatively shallow coastal plateau (3-150 m depth), dominated by sandy substrate with some gravel-dominated areas (Harris and Stokesbury, 2010), with deep submarine canyons on both its eastern and southeastern margins (Stevenson et al., 2004). This system is characterized as highly productive, with strong currents and well-mixed waters. The Mid-Atlantic Bight (MAB) is a relatively flat-bottom, sandy shelf system, with some notable canyons (Stevenson et al., 2004), characterized by seasonal warming that results in strong stratification. The pairing of a strong thermocline and intense ocean currents in the MAB result in annual temperature ranges that are among the most extreme in the world. Annual minimum bottom temperatures span from less than 2°C nearshore and 5°C at the shelf break with maximum temperatures exceeding 16°C near shore and 13°C offshore (Jossi and Benway, 2003). On the shelf, maximum bottom temperatures of 18-19°C during the month of November have been recorded (Richaud et al., 2016).

Due to the large spatial coverage of the sample collection and known variation observed for this species (Gendron, 1992; Shelmerdine et al., 2007; Weetman et al., 2006), samples were partitioned into three geographic regions (Fig. 1). These regions included the northern samples (GB), which were geographically separated from sampling stations within the MAB due to sampling logistics. The other two regions within the MAB are separated by the Hudson Shelf Valley, which opens to Hudson Canyon (Butman et al., 2003; Thieler et al., 2007). The regional delineation within the MAB at Hudson Canyon used in this study is reflective of management regions used in other federally managed benthic invertebrate species (NEFSC, 2014, 2017a,b). The samples to the north of the Hudson Canyon are within the Long Island (LI) region, and those to the south are within the New Jersey (NJ) region (Fig. 1).

2.1 Species range

Samples were collected in partnership with the Northeast Fisheries Science Center (NEFSC) sea scallop assessment surveys and the Virginia Institute of Marine Science (VIMS) sea scallop Research Set-Aside (RSA) cooperative surveys. These surveys use a random-stratified design that spans the continental shelf from Cape Hatteras through Georges Bank and are conducted annually during the summer months (May, June, July). These surveys target the Atlantic sea scallops (*Placopecten magellanicus*) although *B. undatum* are incidentally caught. In 2015, quantitative whelk samples were collected on-board four vessels: the R/V *Sharp* and three commercial scallop vessels. Samples were collected with a lined scallop dredge (Rudders, 2015). Whelk samples were collected from 228 of 798 survey dredge tows. At each sampling station where whelk were collected, all animals were retained and frozen for subsequent analysis.

Extensive sampling in each of the geographical region allowed for the examination of whelk distribution patterns. Ripley's K-function (Ripley, 1977) analysis was performed in R (R Core Team, 2014) to analyze whelk distribution and determine whether they exhibit random, dispersed, or clustered patterns. This analysis evaluates distance r

between particles over the summarized point pattern and compares the observed distribution ($\widehat{K}_{obs}$) with that expected (K_{theo}) from complete spatial randomness (CSR). The '*Kest*' function, within the '*spatstat*' library (Baddeley and Turner, 2005), allows for the visual inspection of estimates from the K-function of the spatial process underlying the distribution of whelk. If the K-function is greater than CSR, this suggests that more points occur close together than would be expected by CSR. If clustering was suggested from this simulation envelope analysis, the maximum absolute deviation (MAD: Ripley, 1977, 1981) test, a formal significance test, was applied. The MAD test provides the absolute value of the largest discrepancy between the estimated ($\widehat{K}(r)$) and simulated K-function ($K_{theo}(r)$) using Besag's transformation of Ripley's K:

$$\mathrm{MAD} = \max_r \left| \widehat{K}\,(r) - K_{theo}(r) \right|.$$

Besag's transformation was used to compare the pattern of whelk distribution within each of the three geographical regions to the null hypothesis of CSR.

2.2 Regional whelk relative abundance per m^2

The dredge was fished for 15 minutes with a towing speed of approximately 3.8-4.0 knots; a Star-Oddi™ DST sensor was used to determine dredge bottom contact time and navigational equipment was used to determine vessel position and speed. Time stamps for both were used to determine sample location and bottom contact time of the dredge. Bottom contact time, dredge width, and vessel location were integrated to estimate gear-specific swept area for each tow in m^2. The relative abundance of whelk was calculated per m^2 by dividing the total whelk collected in a given tow by the swept area of that tow. No estimate of catch efficiency for the survey gear is available; therefore, uncorrected values of absolute catch per swept area are used to estimate minimum relative abundance per m^2 (a likely underestimate as it is not expected that this gear to be highly efficient for whelk). In each geographic region, an average relative abundance per m^2 was calculated from all tows in the given region. Regional abundance estimates were compared using one-way ANOVA and a Tukey's post-hoc test.

2.3 Depth

Two subsets of samples from the LI and NJ regions were used to examine the relationship between relative abundance per m^2 and depth. These sample subsets were delineated perpendicular to the bathymetry of the region to include observations across depths (Fig. 2A). The NJ subset excluded sites south of 38°N due to absence of whelk. No sample subset was examined in GB due to limited number of dredge tows over all depths. For both regions, the relationship between depth and relative abundance per m^2 was examined using a non-linear least square function of the form:

$$\text{relative abundance} = k * e^{-\frac{(\text{depth}-a)^2}{B}}$$

The parameters *a* describes the phase shift of the peak, *B* is the shape parameter describing the width of the peak and *k* represents the height of the curve. This nonlinear function was fit to the relative abundance over depth and used to determine the depth at which a peak in relative abundance is observed.

2.4 Length frequency and sex ratio

Whelk retained during dredge surveys were thawed prior to processing. The body of each whelk was removed from its shell with forceps and shell measurements were taken to the nearest 0.01 mm, using digital calipers.

Length frequency histograms were compared by region and sex using Kolmogorov-Smirnov tests. For each regional length distribution, male and female median lengths were calculated and overlaid on the associated histogram. A subset of all tow samples that caught 20 or more whelk were used to test regional sex ratios; the proportion of females per sample was compared among regions using one-way ANOVA and a Tukey's post-hoc test.

2.5 Size of maturity

The foot of each whelk was gradually removed from its shell using forceps until the collumellar muscle detached. The shell was continually twisted, while pulling on the foot to remove the remainder of the body mass. Each body mass was drained on a paper towel for approximately one minute prior to weighing. Total weight, wet body weight, and dry weight were recorded for each individual. Sex was recorded for each individual and was determined by the presence or absence of a penis, which is located posterior to the right side of the foot folded back within the mantle cavity (Stephenson, 2015). If a penis was present, the length, accounting for the curvature, was measured from base to tip to the nearest 0.01 mm.

Males with a penis length greater than or equal to half of their shell length were considered mature (Gendron, 1992; Køie, 1969; Santarelli and Gros, 1985). For females, the ovary and pallial oviduct (comprised of seminal receptacle, albumen gland, capsule gland, and bursa) were dissected and a combined weight was recorded. Female maturity was determined using a gonadal somatic index (GSI). Female GSI is calculated as follows:

$$\frac{\text{(ovary weight + albumen and capsule gland weight + seminal recpetacle weight + bursa weight)}}{\text{eviserated weight }\left(\text{totaly body weight} - (\text{gonad + digestive gland})\right)}$$

The eviscerated weight is used instead of total body weight in this calculation to avoid inclusion of the variable digestive tract weight (Martel et al., 1986b). Females having a GSI equal to or greater than 0.06 were considered mature (Gendron, 1992; Martel et al., 1986b). Whelk with an atypical gonad as a result of parasite infestation were excluded from the analysis of size of sexual maturity.

Each whelk was classified as either mature or immature as described above. Mature whelk were assigned a maturity condition value of 1, and immature whelk were assigned a maturity condition value of 0. The size of sexual maturity (SOM) is generally defined as the shell length at which the probability of whelk being mature is equal to 0.5 (L_{50}). A logistic regression model was used to determine L_{50} estimates for both sexes and each of the three geographical regions (Roa et. al, 1999; Walker, 2005; R Core Team, 2014), such that the mature proportion of the population at a given shell length (P(L)) is predicted using the following logistic regression model (Roa et. al, 1999; Walker, 2005):

$$\mathrm{P(L)} = \mathrm{P_{max}}\left(1 + \exp^{-\ln(19)\left(\frac{\mathrm{L}-\mathrm{L_{50}}}{\mathrm{L_{95}}-\mathrm{L_{50}}}\right)}\right)^{-1}$$

where P_{max} is the maximum proportion of mature whelk, and L_{50} and L_{95} are lengths at which 50% and 95% of the whelk are in mature condition. Confidence intervals were added to the estimate of L_{50} by bootstrapping the generalized linear model for 10,000 runs with replacement (Hastie et al., 2009). Maturity curves were fit using an R-script adapted from Harry (2013), which has also been utilized by Haig et al. (2015), Hollyman

(2017), and Stephenson (2015), and significance was tested by comparing the amount of deviance explained relative to the null model using chi-squared tests.

2.6 Meta-analysis of whelk fisheries

Fisheries assessment reports and the primary literature wherein studies examining SOM for *B. undatum* were assembled. From these reports, and building on the SOM data compiled by Haig et al. (2015), reported SOM estimates along with complimentary metadata including sex, approximate location, average sampling depth, method used to assess maturity (if available), and MLS regulations for that country were compiled. These data were used to assess both large- and small-scale spatial variability in SOM and associated MLS regulations. The SOM values from this present study were then compared to those reported elsewhere.

3. Results

3.1 Species range

The distribution of samples collected allowed the extent of depth and latitudinal range for the species to be mapped (Fig. 1). Presence (tows that caught one or more whelk) and absence (tows that caught zero whelk) pattern shows that most whelk were found at stations in water depths between 40 and 75 m, and that their southern limit appears to be close to 38°N.

For the Ripley's K tests, the relationship between empirical K-function $\widehat{K}_{obs}(r)$, calculated from the data, and theoretical K-function K_{theo}(r) provide a visual assessment of the distribution pattern. In all three geographical regions, the empirical curve was higher than the theoretical curve, $\widehat{K}_{obs}(r) > K_{theo}(r)$, suggesting that a typical point has more neighbors than expected in a completely random pattern (Supplementary Appendix A). Statistical evaluation of these patterns using the MAD test indicated that in all three geographical regions there is strong evidence that waved whelk are not randomly distributed, and suggest a clumped pattern (p-value [all three regions] =0.01, MAD statistic: GB=0.195; LI=0.094; NJ= 0.249).

3.2 Regional whelk relative abundance per m^2

No significant difference in relative abundance per m^2 was detected between the three geographical regions (GB:LI, p=0.17; LI:NJ, p= 0.99; GB:NJ, p=0.06). However, a trend emerged with relative abundance and latitude such that relative abundance per m^2 increased with latitude. Georges Bank had an average regional relative abundance per m^2 of 0.0026 individuals m^{-2} (σ=0.014, n=194), Long Island had 0.0012 individuals m^{-2} (σ=0.004, n=179), and New Jersey had 0.0012 individuals m^{-2} (σ=0.004, n=425).

3.3 Depth

Tow depths ranged from 26.5 to 77.6 m in LI and from 32.1 to 95.9 m in NJ; whelk were not found at all depths and these ranges appear to encompass an inshore and offshore limit (Fig. 2B). The peak abundance per m^2 was at 51.3 m in LI and 59.5 m depth in NJ (Fig. 2B).

3.4 Length frequency and sex ratio

3.4.1 Length frequencies

Length frequency distributions varied among geographic regions, and by sex. The null hypothesis that the samples are drawn from the same distribution between sites was rejected for all pair comparison between geographic regions (p <0.001, GB: LI, D=0.19;

$p << 0.001$, GB: NJ, D=0.22; $p << 0.001$, LI: NJ, D=0.21). Similarly, the null hypothesis that the samples are drawn from the same distribution for males and females in each geographical region was rejected ($p=0.02$, GB: D=0.13, $p < 0.001$, LI: D=0.23, $p << 0.001$, NJ: D=0.33) (Fig. 3).

Median lengths of females were larger than males in each geographic region. The difference in the median lengths between females and males (median female length minus median male length) progressively increases from north to south, with a minimal difference, 2 mm, in Georges Bank, 3.2 mm in Long Island, and the greatest difference, 5.8 mm, in New Jersey.

3.4.2 Sex ratio

The sex ratio was significantly different from 1:1 in New Jersey (63% female, $\sigma=0.10$, $p << 0.001$, df=35). However, it did not significantly deviate from 1:1 in either Georges Bank (54% female, $\sigma=0.11$, $p=0.11$, df=10) nor Long Island (50% female, $\sigma=0.16$, $p=0.47$, df=11). The post-hoc Tukey's HSD test showed that the proportion of females in New Jersey and Long Island were significantly different ($p=0.009$), all other comparisons were not significant (GB: LI, $p=0.69$; GB:NJ, $p=0.12$).

3.5 Size of maturity

Maturity at length curves for males and females in the three geographical regions were all highly significant when tested against the null model (Fig. 4). Significant regional and sex differences are evident in the SOM (analysis of deviance [region and sex] $p < 0.001$). Northern samples, from the GB region, tend to mature at a largest size (male: 67.8 mm, female: 72.8 mm). In the Long Island region, females have the smallest SOM observed (male: 57.5 mm, female: 59.4 mm). In the New Jersey region the males have the smallest SOM observed (male: 56.8 mm, female: 64.3 mm). In all three regions, males tend to mature at a smaller size than females, with male SOM ranging from 56.8 – 67.8 mm, and female SOM ranging from 59.4 – 72.8 mm (Fig. 4).

3.6 Meta-analysis of whelk fisheries

SOM estimates from exploited waved whelk stocks are highly variable, ranging from 41.8 – 86 mm for males (Supplementary Appendix B), and 44.8 – 101 mm for females (Supplementary Appendix C). For all the stocks examined in this review, the median size of maturity estimate for waved whelk is approximately 62.8 mm for males and 68.1 mm for females. These size of maturity estimates for 90% of male and 92.3% of female estimates are greater than their associated minimum landing sizes (Fig. 5).

4. Discussion

B. undatum populations in the U.S. portion of the Northwest Atlantic, as reported for Georges Bank through southern New Jersey, show regional variability in length distribution, sex ratio, and size of sexual maturity. In addition to the observed differences in life history characteristics, this study is the first to document the spatial distribution of waved whelk in this region, with the whelk resource well defined in the New Jersey and Long Island regions. In the Mid-Atlantic, the stock appears to be concentrated in water depths between 40 and 75 m, and was not found south of approximately 38°N. No samples were taken in the region of Block Island, south of Georges Bank, and lower sampling effort in the Georges Bank region resulted in less information about whelk distribution there. Likewise, all samples were collected during summer surveys and may not reflect year round habitat use for the species.

Aggregation has been commonly observed in studies of marine benthic invertebrates, and has been demonstrated for other gastropods (Heip, 1975; Kosler, 1968). This dredge sampling study design allowed comparison of spatial patterns in whelk distribution, unlike past studies, which used baited pots that may bias spatial distributions by increasing aggregation. The implied clustering in the three geographical regions may be a reflection of this species' limited movement on large spatial scales. Weetman et al. (2006) found *B. undatum* exhibits a widespread population structure, with microsatellite variation differentiation over short distances, as well as across the Atlantic, and between Europe and Canada. The waved whelk populations within Georges Bank and the MAB should be examined further to identify if this aggregation pattern is echoed by population genetic structures in these regions.

The survey was able to provide extensive sample coverage, with sampling depths ranging from 13 to 112 m. Whelk were obtained in samples from a minimum depth of 27.4 m to a maximum depth of 112 m, but were concentrated between 40-75 m in the MAB. Within its known range, this species is commonly found from the lowest part of the intertidal zone to 200 m, and have been found at depths greater than 1,000 m (Nielsen, 1974; Morel and Bossy, 2004; Thomas and Himmelman, 1988). Although, occasionally found in deep water (>30 m) (Fretter and Graham, 1985), *B. undatum* has shown a preference for water around 20 to 30 m deep (Ellis et al., 2000; Valentinsson et al., 1999) When examining the relationship between depth and relative abundance, this study revealed that the whelk in the MAB have a preference for slightly deeper habitat than other studies published (LI: 51.3 m; NJ: 59.5 m). A deeper depth preference for waved whelk in the Mid-Atlantic may be associated with the species' optimal temperature range and habitat type. The theoretical optimum temperature range for *B. undatum* growth is believed to be between approximately 8-18°C (Hollyman, 2017), with adverse responses to elevated temperatures, and 29°C proving to be lethal (Gowanloch, 1927). Point-measurements of temperature were taken during the timed dredge tows, and provide a snapshot of bottom temperatures experienced by whelk in these regions during the sampling period. All regions experienced temperature below the theoretical optimum, with median temperatures ranging from 8.0°C in Georges Bank, 4.7°C in Long Island, 7.1°C in New Jersey, and bottom temperatures in the MAB are known to range from 2° to 19°C annually. Additionally, *B. undatum* can be found in almost all habitat types, with preference for sandy and stony substratum (Schäfer, 1956; Nielsen, 1974), both of which are common in the regions sampled within the Mid-Atlantic.

The observed habitat preference of this carnivorous whelk at deeper depths could be related to major commercial concentration of Atlantic sea scallops that occurs on Georges Bank and the MAB between depths of 35 and 100 m (Hart and Rago, 2006). In that fishery, scallops are shucked at sea with only the adductor muscle (meat) retained and the remainder (shell and viscera) is discarded overboard (Hart and Rago, 2006; NEFMC, 1993; NEFSC, 2014). Scallop shell may act as hard substrate (Hancock, 1967; Heude-Berthlin et al., 2011), which may serve as egg attachment habitat for egg-laying females. Additionally, *B. undatum* feed mostly on bivalves, and occasionally on polychaetes, echinoderms and dead fish (Garcia et al., 2006; Himmelman and Hamel, 1993; Mercier and Hamel, 2008; Nielsen, 1974). Whelk use their keen olfactory senses to locate bivalve carrion (Rochette and Himmelman, 1996). The heavy concentration of scallops in Georges Bank and the MAB, and the discarded meat from the commercial fishery may serve as a food source for the whelk.

Density estimates for waved whelk, ranging from 0.06 – 0.38 individuals m^{-2} (Kidney, 1993; Valentinsson et al., 1999) have been calculated using catch from baited pots. Capture data from pots may not be an adequate method for estimating whelk population density because pots are highly size selective, and catchability may vary as a function of size due to factors such as mobility, dietary preference with size, season of sampling. Some studies that estimated whelk densities only include large whelk (>60 cm) in density calculations, potentially underestimating total individuals within the population (e.g., Himmelman, 1988; McQuinn et al., 1988). Likewise, the catch in baited pots would vary by bait type and soak time, and estimates of density rely on highly uncertain calculation of the estimated area of attraction (McQuinn et al., 1988). Other methods that have been used to estimate density include SCUBA diving, with estimates ranging from 0.05 – 2.86 individuals m^{-2} (Himmelman, 1988; Jalbert et al., 1989; Kidney, 1993). However, this method is limited in the scale of area that can be surveyed. For instance, Jalbert et al. (1989) surveyed shallow water communities (lowest level of spring tide to 20 m) in a northern portion of the Gulf of St. Lawrence; this diving method would be much less successful in deeper water continental shelf regions. Additionally, using SCUBA diving to survey abundance does not account for whelk below the surface of the substrate. Whelk are known to spend much of their time buried in soft sediment (Himmelman, 1988), thus visual counts likely underestimate whelk present. Underwater television optical surveys (0.33 ± 0.05 individuals m^{-2}) and mark-recapture (0.49 – 1.94 individuals m^{-2}) have also been used (Kideys, 1993). These methods are highly selective for larger individuals and whelk less than 55 mm are not included in density estimates. The underwater television method provided overestimates of density due to the inclusion of different whelk species and dead Buccinum (Kideys, 1993). Mark-recapture proved to be unreliable due low recapture rates after tagging (Kideys, 1993). Additionally, this tagging process disturbs and stresses marked individuals, which may result in different behaviors from undisturbed whelk (Sainte-Marie, 1991).

The abundance estimates provided by this study may be more realistic estimates over a wider area than those estimated using baited pots. Dredge catches provide a better representation of general relative abundance estimates over a larger spatial scale than baited pots in areas of clumped whelk populations providing that the catch-efficiency of *B. undatum* over the entire size-range is investigated and understood. However, Powell and Mann (2016) highlight that hydraulic dredges consistently underestimate the biomass of benthic infauna on the continental shelf, especially if the large specimens are patchy in their distribution. Because no efficiency correction is available to apply to the absolute catch numbers reported herein, the relative abundance estimates are also likely an underestimate of the true abundance.

In this study, relative abundance estimates did not significantly differ among geographical regions. However, a trend of increasing relative abundance with increasing latitude was observed. Of the three geographic regions surveyed, the highest relative abundance was observed in the northern-most region, this result agrees with other studies performed in North American waters, *B. undatum* attained greatest densities in the colder regions (Jalbert et al., 1989; Himmelman, 1991). Recalculations of the relative abundance per m^2 were made using only sample stations located within the observed whelk range (between depths of 40–75 m and north of 38°N latitude) in the MAB. This resulted in higher estimates (LI= 0.0015 individuals m^2, σ=0.004, n=145; NJ= 0.0018 individuals m^2, σ=0.005, n=286). These may prove to be more precise estimates due to the exclusion of sampling sites outside of the observed whelk range in the MAB.

Shell length of adult whelk varied by latitude, and a trend of decreasing shell length southward was evident among the regions examined. This trend was greater for males than females. Thermal limitations could be responsible for this apparent regional trend in lengths. First, waved whelk are a boreal species (Golikov, 1968; Levitan and Lavrushin, 2009), and the southern-most region in this study is characterized by the warmest water temperatures, which may limit maximum body size. Around the English coast, where whelk are near their southern limit in the Northeast Atlantic, warmer temperatures are thought to be a limiting factor for growth and reproduction (McIntyre et al., 2015). An analysis of 14 marine invertebrate species, from six phyla (including *Nacella concinna*, a marine gastropod) revealed that smaller individuals survived at higher temperatures relative to their larger conspecifics in acute temperature treatments, suggesting that smaller body size is a physiological advantage to withstand warmer water temperatures (Peck et al., 2009). Observed regional variation in shell characteristics, such as shell length, can likely be attributed to a combination of factors such as temperature, depth, predation pressure (Thomas and Himmelman, 1988) and could suggest genetic differences (Magnúsdóttir, 2010).

Within the New Jersey region, the sex ratio of whelk during the early summer months appear to be disproportionately skewed towards females. Reported sex-ratios for waved whelk in other parts of the world show both balanced male: female ratios (Heude-Berthelin et al., 2011), as well as sex ratios that were unbalanced (Fahy et al., 2000;

Kenchington and Glass, 1998). Generally, when skewed sex-ratios are observed, females dominate the samples, but occasionally populations are observed with male dominated sex ratios (Fahy et al., 2000; Kenchington and Glass, 1998). Deviations from a 1:1 sex ratio could be due to sample timing (Hollyman, 2017). Females seeking appropriate egg-laying habitat may congregate and thereby appear to dominate the sex ratio. Alternatively, females may not appear in the catch (if baited pots were used) because they are not attracted to food during egg laying (Hollyman, 2017). Martel et al. (1986a, 1986b) suggested the reproductive period of copulation and egg laying in Quebec was between May through September. Likewise, the female-dominated sex ratio observed in New Jersey may simply be related to increased female mobility which would cause them to be more susceptible to the dredge at the time of the survey compared to immobile males that may be in the sediment and less available to the dredge. Collectively, this may suggest that the May through July survey period falls near the reproductive season for waved whelk in the Mid-Atlantic, particularly the New Jersey region.

In general, male whelk in the Mid-Atlantic tend to mature at a smaller size than most other stocks (with Georges Bank being an exception). However, female whelk in the three geographical regions examined tended to mature at a larger size than most other stocks (with Long Island being an exception) (Supplementary Appendices B, C). Driving forces behind variability in size of maturity among populations has not been fully resolved in the literature. A range of environmental factors may influence size of maturity and body size in gastropods, including temperature (Hollyman, 2017), depth (Olabarria and Thurston, 2003), predation pressure and food availability (Fahy et al., 2006; Gendron, 1992). Extreme seasonal temperature variation occurs along the Mid-Atlantic continental shelf; therefore, repeated sampling at different times of the year should be carried out to test effects of temperature and its influences on size of maturity. Likewise, it is important to note, when comparing female SOM estimates from different studies, reproductive cycles are known to vary regionally which could influence the conclusions drawn. Additionally, whelk samples have been obtained several gear types, at different depth ranges, different temperature ranges, and on different substrate types, which could also affect observed SOM. SOM estimates have also been calculated using several methods. Collectively, these varying approaches could lead to different size of maturity estimates from one study to another.

Size of sexual maturity varied significantly among the Mid-Atlantic regions and by sex. Females consistently matured at a larger size than males. This result is consistent with findings along the Brittany coast of France (Heude-Berthelin et al., 2011); yet differ from other studies where no apparent sex-specific difference in size of sexual maturity was found (Valentinsson et al., 1999). Additionally, contrary to our result, Hollyman (2017) found that males matured at a larger size than females that in six sites within the U.K.. However, there is intense commercial fishing pressure in the U.K., which has been occurring for a prolonged period (Heude-Berthelin et al., 2011). This long-standing fishing pressure may have selectively removed larger females resulting in a shift in size of maturity to a smaller size in females bringing the size of maturity closer for males and females. However, these studies used different methods for examining size of sexual maturity, including histology (Heude-Berthelin et al., 2011), microscopic analysis and penis length (Valentinsson et al., 1999), and visual inspection and penis length

(Hollyman, 2017). Differences in methodology could lead to the differences in maturity estimates due to variation in the level of accuracy among methods.

To date, no formal fishery management plan exists for *B. undatum* in the U.S. A possible approach to sustainable management would be to ensure that the fishery does not target individuals that have yet to spawn at least once (those smaller than the size of maturity). This strategy would minimize fishing impacts on whelk below the SOM, and allow retention of individuals that have already contributed to the spawning stock. The long-term productivity and sustainability of this fishery relies on maintaining a healthy spawning stock and level of recruitment. If the MLS is set lower than the size of maturity, the size limit may not protect the population. However, if the size limit was set at an appropriately large size (i.e. above size of maturity), but there were few individuals at that size, the fishery would have limited exploitable biomass on which to fish. In each MAB region the median length falls above the estimated size of sexual maturity for both sexes (Fig. 4B), as would be expected in a lightly exploited stock. This suggests that there are mature individuals in each geographic region that would be available to the fishery, should a fishing size limit be set at or above the SOM.

Overall, the waved whelk populations in the Mid-Atlantic are currently largely unexploited and few stakeholders would suffer economic losses due to implementation of fisheries regulations. Because of the strong spatial variability in population characteristics observed in this study, fishery managers should take into consideration region-specific options to protect fishable populations. Continued research is needed to further investigate the stock at sub-regional levels, and to examine growth, genetic structure, and interactions with the environment.

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Figure Captions

Figure 1: Map of the study region, Mid-Atlantic Continental Shelf, including both Georges Bank and Mid-Atlantic Bight. Three geographical regions delineated by dashed lines (Georges Bank, Long Island, and New Jersey). Locations of each survey dredge tow shown with circles; grey circles indicate sample tows in which whelk were present, white circles show sample tows where whelk were absent.

Figure 2: A. Map of the Long Island and New Jersey sample subsets used for the examination of the relationship between depth and relative abundance per m^2. The samples included each region are shown with LI in black, and NJ in gray. B. Relationship between depth and relative abundance for LI (left panel) and NJ (right panel). The best non-linear least-square function for each region is overlaid in grey.

Figure 3: Length frequency distributions for males (dark bars) and females (light bars) in three regions sampled: Georges Bank (left panel; male: n=234, females: n=285), Long Island (center panel; males: n=437, females: n=389), and New Jersey (right panel; males: n=764, females: n=1070). Median lengths for males (solid lines) and females (dashed lines) are shown for each region.

Figure 4: A. Regional population maturation probability for waved whelk in the Mid-Atlantic with associated bootstrapped 95% confidence error (shaded band). Logistic regression model fits to maturity by length, location (Georges Bank, Long Island, and New Jersey) and sex (left, males; right, females). B. Shell length (mm) at which 50% of

the population is mature by geographical regions and sex, with associated 95% confidence limits. Median length for each region and sex has been overlaid with the dotted line.

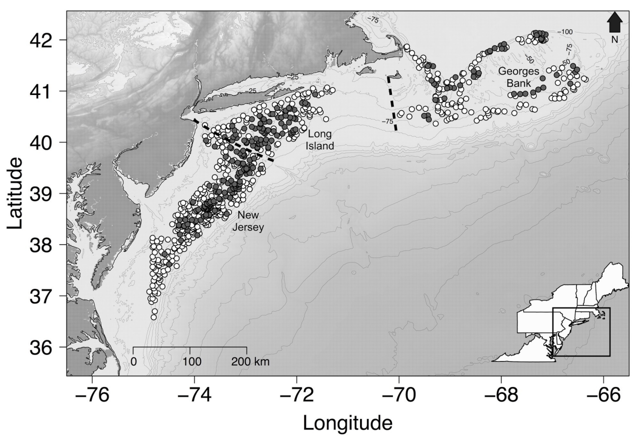
Figure 5: Size of maturity for male and female whelk obtained from published literature and assessment reports of waved whelk populations. The 95% confidence intervals (if available) are provided, and data are grouped by country, then latitude. Minimum landing size enforced in each country is represented with the heavy black line.

Appendices Captions

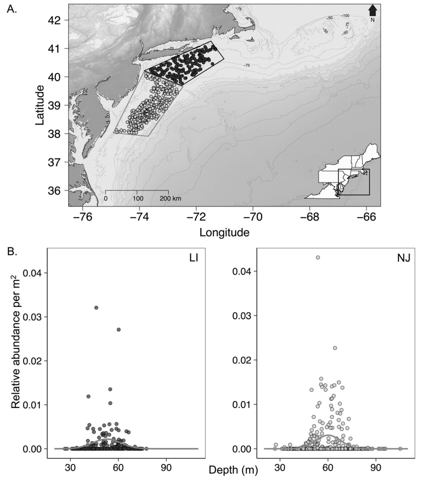
Appendix A: K-function for all three regions sampled: Georges Bank (left panel), Long Island (center panel), and New Jersey (right panel). The estimated function for each region (solid line), $\widehat{K}_{obs}(r)$, is compared to the theoretical function (dotted line), $K_{theo}(r)$, under CSR. Simulation envelopes are shown in grey, calculated from 100 simulations of the K-function.

Appendix B: Data used to calculate male comprehensive size of maturity median and quartiles. Data from published literature, when available. If other data (latitude, longitude) were not provided, approximate sample locations were calculated in Google Earth. Data arranged by size of maturity. Data separated into 4 quartiles (25^{th}, 50^{th}, 75^{th}, 100^{th}) by solid lines.

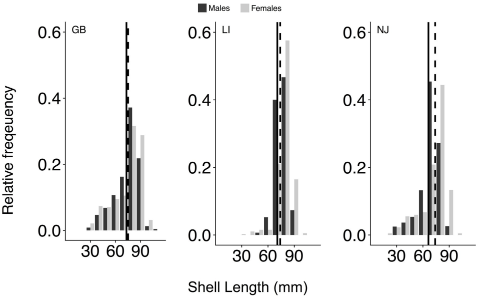
Appendix C: Data used to calculate female comprehensive size of maturity median and quartiles. Data from published literature when available. If other data (latitude, longitude) were not provided, approximate sample locations were calculated in Google Earth. Data arranged by size of maturity. Data separated into 4 quartiles (25th, 50th, 75th, 100th) by solid lines.



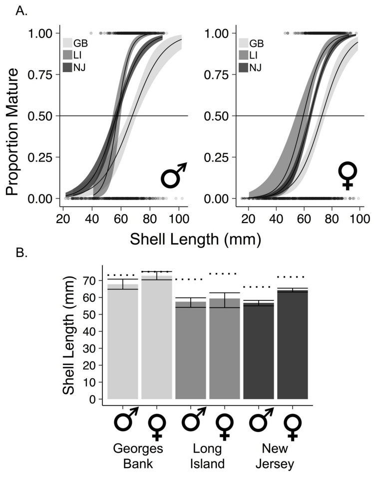
N
Georges
Bank
Long
Island
New
Jersey
-25
-50
-75
-100
0
100
200 km
Latitude
Longitude
42
41
40
39
38
37
36
−76
−74
−72
−70
−68
−66

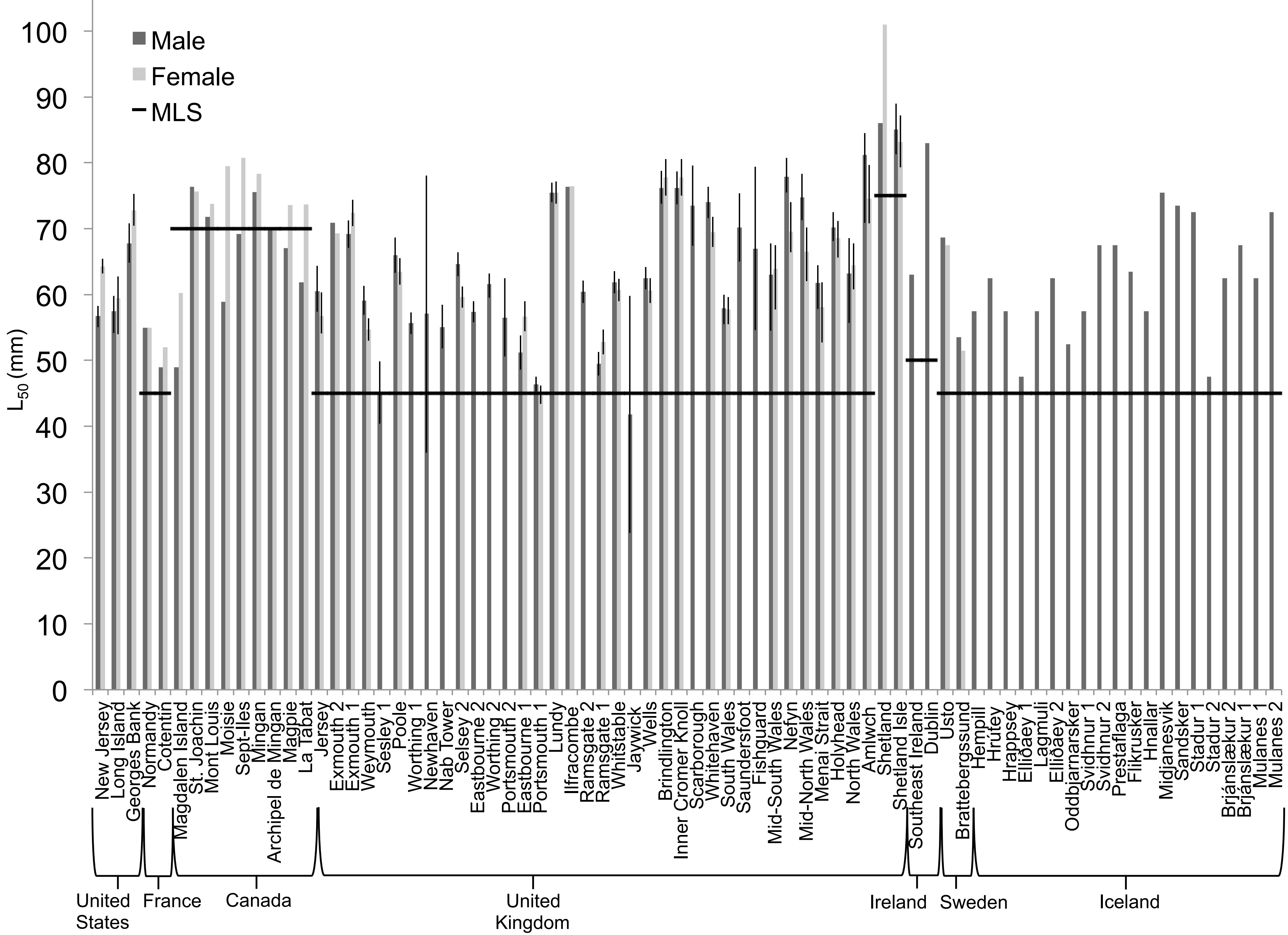


A.
Latitude
Longitude
N
0
100
200 km
B.
Relative abundance per m²
Depth (m)
LI
NJ



Males
Females
GB
LI
NJ
Relative freqeuency
0.0
0.2
0.4
0.6
30
60
90
Shell Length (mm)


A.
Proportion Mature
1.00
0.75
0.50
0.25
0.00
GB
LI
NJ
20
40
60
80
100
Shell Length (mm)
B.
Shell Length (mm)
70
60
50
40
30
20
10
0
Georges Bank
Long Island
New Jersey



Male
Female
MLS
L50 (mm)
0
10
20
30
40
50
60
70
80
90
100
New Jersey
Long Island
Georges Bank
Normandy
Cotentin
Magdalen Island
St. Joachin
Mont Louis
Moisie
Sept-Iles
Mingan
Archipel de Mingan
Magpie
La Tabat
Jersey
Exmouth 2
Exmouth 1
Weymouth
Sesley 1
Poole
Worthing 1
Newhaven
Nab Tower
Selsey 2
Eastbourne 2
Worthing 2
Portsmouth 2
Eastbourne 1
Portsmouth 1
Lundy
Ilfracombe
Ramsgate 2
Ramsgate 1
Whitstable
Jaywick
Wells
Brindlington
Inner Cromer Knoll
Scarborough
Whitehaven
South Wales
Saundersfoot
Fishguard
Mid-South Wales
Nefyn
Mid-North Wales
Menai Strait
Holyhead
North Wales
Amlwch
Shetland
Shetland Isle
Southeast Ireland
Dublin
Usto
Brattebergssund
Hempill
Hrúfey
Hrappsey
Elliðaey 1
Lagmuli
Elliðaey 2
Oddbjarnarsker
Svidhnur 1
Svidhnur 2
Prestaflaga
Flikrusker
Hnallar
Midjanesvik
Sandsker
Stadur 1
Stadur 2
Brjánslækur 2
Brjánslækur 1
Mulanes 1
Mulanes 2
United States
France
Canada
United Kingdom
Ireland
Sweden
Iceland